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Biogeographical patterns of soil microbial community as influenced by soil characteristics and climate across Chinese forest biomes

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ABSTRACT

Soil microorganisms form an important component of the Earth's biosphere and play an integral role in carbon, nitrogen and phosphorus cycling. Several biotic and abiotic factors affect the biogeographical distributions of soil microbial biomass (MB) and communities on geographical scales; however, the extent to which soil microbial communities are influenced by these factors is not yet clear. We examined and compared the biomass and structure of soil microbial communities within and between nine mature undisturbed forest ecosystems along the 3700-km North-South Transect in Eastern China (NSTEC). The results showed that soil MB and phospholipid fatty acids (PLFAs) increased with latitude. The structure of the microbial community in boreal forest soils was comparable with that in temperate forests but was significantly different from the microbial communities in warm temperate, subtropical and tropical forests. The mean annual temperature, soil organic carbon, soil total nitrogen and soil easily soluble phosphorus were the main predictors of latitudinal variance in the soil microbial communities. Soils within the same climatic types had similar properties, and soil MB and PLFAs seemed to change along gradients in the various forest types along the NSTEC. Microbial communities showed spatial variation and were dependent on soil properties and climate but were relatively independent of plant functional traits and litter quality. The results suggested that soil microbes could improve the ecosystem models so that they simulate the microbial mechanisms of carbon (C) and nutrient cycling.

1. Introduction

Soil microorganisms play a pivotal role in the earth's biogeochemical cycles (Falkowski et al., 2008; Tu et al., 2016). While we know that soil microbial communities vary across geographical space, with possible consequences for geochemical cycling, we have limited information about the biogeographical distribution of these communities. It restricts our ability to simulate and predict the microbial mechanisms that control carbon (C), nitrogen (N) and phosphorus (P) cycling. As highlighted by Luo et al. (2016), information about the large-scale distributions and structures of soil microbial communities would help reduce the uncertainties associated with earth system models. We therefore need an improved appreciation of the spatial patterns of, and the factors that control, soil microbial biomass (MB) and communities (Balser and Firestone, 2005).

Microbial biomass, an important living part of soil organic matter, is mainly comprised of soil C and N. Numerous studies have confirmed that spatial variations in soil MB are the result of spatial heterogeneity in soil properties and climate conditions (Marinari et al., 2006; Xu et al., 2013). These spatial variations in soil MB among biomes reflect its ability to respond rapidly to environmental change (Marinari et al., 2006); for example, soil MB increases as latitude increases, and also as soil organic C density and below-ground plant biomass increase (Xu et al., 2013; Li et al., 2014). Soil MB mainly consists of bacteria, archaea and fungi with diameters of less than 500 μm. Different microbial species are involved in a range of ecosystem functions. For example,

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most bacteria do not, but fungi do, exude enzymes for decomposing complex C compounds. Therefore, information about the spatial distribution of soil microbial biomass at the regional scale is needed to support examinations of soil microbial biogeography (Martiny et al., 2006) and for global nutrient cycling (Allison et al., 2010).

Similar to macro-organisms, soil microbes can be used as indicators of biogeography because of their diversity, functional traits, dispersal ability and density (Fierer et al., 2007; Tu et al., 2016; Zhou et al., 2016). For example, Tu et al. (2016) reported that the different forests along a latitudinal gradient harbored markedly different soil diazotrophic communities and that the biogeographic patterns of the soil communities resembled those of the plants and animals. The variations in the diversity and richness of soil bacterial communities along climatic gradients (Zhou et al., 2016) and between ecosystem types (Fierer and Jackson, 2006) also highlight spatial patterns in soil microbes. While earlier studies have highlighted variations in the structures of microbial communities with latitude (Zhou et al., 2008; Ghiglione et al., 2012; Tedersoo and Bahram, 2014), we still do not have a clear picture of how soil microbial communities vary along geographical gradients or which factors control geographical patterns at different scales. The structures of microbial communities are intimately linked to their roles in ecological processes, and these relationships are one of the central issues in ecological theory (Loreau et al., 2001; Talbot et al., 2014). With an improved understanding of the geographical patterns in the structures of soil microbial communities, we could predict the functional attributes or functional diversity of these soil microbial communities (Cao et al., 2016); this would represent an important step towards the development of a generalized framework for simulating and predicting microbial mechanisms that contribute to ecosystem functioning at the regional scale.

Spatial variations in soil microbial communities may be affected by biotic and abiotic factors (Fierer and Jackson, 2006; Cao et al., 2016), and the influences of these factors may vary at regional, continental and global scales (Tu et al., 2016). Previous studies reported that the composition and diversity of microbial communities were positively correlated with soil pH (Shen et al., 2013), carbon/nitrogen ratio (C/N) (Fierer and Jackson, 2006), multiple year mean annual temperatures (MAT) and precipitation (MAP) (De Vries et al., 2012; Tedersoo et al., 2012; Cao et al., 2016; Tu et al., 2016). Plant functional traits have also been reported to modify soil microbial communities by altering the quantity and quality of nutrient inputs (Orwin et al., 2010), and soil physical and chemical properties (Brussaard et al., 2007; Thoms et al., 2010). The LDMC and the leaf C/N ratio, combined with tree growth rates, had a positive influence on the abundances of specific microbial functional groups (Pei et al., 2016). However, most previous investigations of the relationships between plant functional traits and microbial communities have only considered a few plant species traits, so our understanding of the relative importance of the different traits is limited. The main controls on geographical patterns of soil microbes remain unclear, because, to date, few researchers have dealt adequately with the individual and interactive effects of climate, plant functional traits and soil substrate availability on soil microbial communities at the large scale.

The North-South Transect of Eastern China (NSTEC) extends from a cold-temperate coniferous forest in the north to a tropical rain forest in the south, and includes almost all forest types in the Northern Hemisphere (Zhang and Yang, 1995) (Fig. 1 and Table 1). This transect therefore provides the optimal setting for investigations of geographical patterns of microbial communities and their responses to environmental change at the large scale. In this study, we determined the compositions of soil microbial communities using phospholipid fatty acids (PLFAs) and examined the effects of climate, soil conditions, plant functional traits and litter properties on the structures of soil microbial communities across nine mature undisturbed forest ecosystems at different latitudes along the 3700-km NSTEC. The aims of this study were to determine (1) the latitudinal patterns of soil MB and different groups of microbial PLFAs; and (2) the relationships between climate, soil properties, plant functional traits, litter properties and microbial PLFA biomass at the large scale.

2. Materials and methods

2.1. Study area

The NSTEC is the 15th standard transect of the International Geosphere-Biosphere Program (IGBP). It extends from Hainan Island in the south to the northern border of China, and includes 25 provinces and approximately 1/3 of China. Because of the influence of the eastern Asian monsoon, the climate along the NSTEC differs from the climates experienced at similar latitudes in Europe and North America, and is characterized by clear latitudinal gradients in temperature and precipitation. Different types of zonal forest ecosystems are distributed along the NSTEC from north to south, including cold-temperate coniferous forests, temperate mixed forests, warm-temperate deciduous broad-leaved forests, subtropical evergreen broad-leaved forests and tropical monsoon rainforests (Zhang and Yang, 1995; Yu et al., 2006).

We selected nine forest ecosystems along the NSTEC, namely Huzhong (HZ), Liangshui (LS), Changbai (CB), Dongling (DL), Taiyue (TY), Shennong (SN), Jiulian (JL), Dinghu (DH) and Jianfeng (JF) (18°44′–51°46′ N, 128°53′–108°51′E) (Fig. 1, Table 1). Together, they span 33° of latitude from 18 to 51 °N and extend over a distance of more than 3700 km. These ecosystems represent the primary zonal forest ecosystems in China, i.e. temperate coniferous forest, broad-leaved Korean pine forest, deciduous broad-leaved forest, evergreen broad-leaved forest, monsoon evergreen broad-leaved forest and tropical rain forest. Our study forests were natural and had not been subjected to logging or harvesting activities in the last hundred years. According to the U.S. soil taxonomy, the main soils in the forests were Spodosols (HZ), Albi-Boric Argosols (LS and CB), Alfisols (DL and TY), Inceptisols (SN) and Ultisols (JL, DH and JF) (Table 1, Soil Survey Staff, 2010). The soils in HZ, LS, CB and TY were silt; those in SN, JL, DH and JF were silt loams, and the soil in DL was sandy loam (Soil Survey Staff, 2010).

2.2. Soil sampling

Soil samples were collected from four random plots in each study site in July and August 2013. The plots measured 30 × 40 m, and were separated from adjacent plots by a 10 m buffer zone. The four plots at each site had identical vegetation. Mineral soil samples were collected from the soil surface (up to 10 cm deep) at between 30 and 50 points in each plot along an S-shape using a coring device with a diameter of 6 cm. The above-ground standing biomass, dead plant parts and litter were removed from each sampling point before extracting the sample. The soil samples from each plot were pooled together as a composite sample. Visible roots and residues were removed before the fractions of each sample were homogenized. We stored the samples at 4 °C in a portable refrigerator during field sampling. Once back at the laboratory, the fresh soil samples were immediately sieved through a 2-mm mesh and were subdivided into two subsamples. One subsample was stored briefly at 4 °C until analysis for soil physical and chemical properties. Another was stored briefly at −20 °C until analysis for phospholipid-derived fatty acids (PLFAs).

2.3. Soil analyses

2.3.1. Soil chemical analyses

Soil pH was measured on a soil to water suspension at a ratio of 1:2.5 *v:v* using a pH digital meter (Iovieno et al., 2010). Soil moisture (SM) was measured gravimetrically on 20 g of fresh soil that had been oven-dried at 105 °C to constant weight as soon as we returned to the laboratory. Soil temperature (ST) was measured *in situ* with a rectangular geo-thermometer. Soil organic carbon (SOC), total N (TN), litter

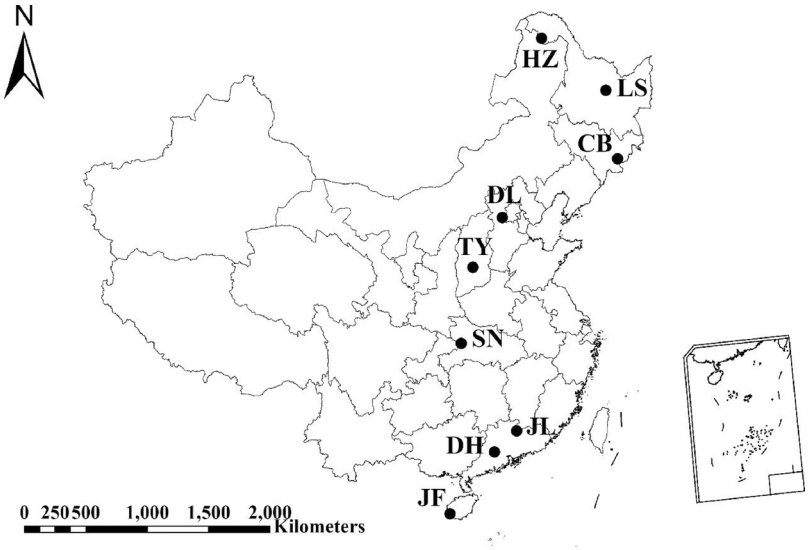

Fig. 1. Distribution of typical forest ecosystems along the North-South Transect in Eastern China (NSTEC). The names of the sampling sites from north to south were abbreviated as followed: HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng.

total C (litter TC) and litter total N (litter TN) were measured with an element analyzer (Elementar, Vario Max, Germany). Soil easily soluble phosphorous (easily soluble P) was extracted by sodium bicarbonate and determined by spectrophotometry (Olsen et al., 1954). Soil microbial biomass carbon (MBC) and nitrogen (MBN) were measured by the chloroform fumigation and direct extraction technique. The silt fractions (< 53 μm) were separated by wet-sieving and then were freeze-dried, as outlined by Six et al. (2000). The soil properties are shown in Table 2.

Table 1
Summary of the main characteristics of the sampling sites along the NSTEC.

Sampling Sites	Longitude (E)	Latitude (N)	Elevation (m)	MAT[b] (°C)	MAP[b] (mm)	Vegetation types	Dominant tree species	Soil type
HZ[a]	123°01′12″	51°46′48″	850	−3.7	473	Cold temperate coniferous forest	*Larix gmelinii* *Pinus koraiensis Nakai* *Betula platyghylla* *Populus davidiana*	Spodosols
LS	128°53′51″	47°11′06″	401	0.01	648	Temperate conifer broad-leaved mixed forest	*Pinus koraiensis* *Pinus koraiensis Nakai* *Fraxinus mandshurica Rupr* *Betula costata*	Albi-Boric Argosols
CB	128°05′27″	42°24′16″	758	2.8	691	Temperate conifer broad-leaved mixed forest	*Pinus koraiensis,* *Acer tegmentosum*	Albi-Boric Argosols
DL	115°25′24″	39°57′27″	972	6.6	539	Warm temperate deciduous broad-leaved forest	*Quercus liaotungensis* *Ulmus* spp.	Alfisols
TY	112°04′39″	36°41′43″	1668	6.0	644	Warm temperate deciduous broad-leaved forest	*Quercus liaotungensis* *Populus davidiana* *Betula platyphylla*	Alfisols
SN	110°29′43″	31°19′15″	1510	8.5	1447	Subtropical deciduous evergreen mixed forest	*Fagus engleriana* *Cyclobalanopsis glauca*	Inceptisols
JL	114°26′28″	24°35′05″	562	18.2	1770	Subtropical evergreen broad-leaved forest	*Machilus nees* *Castanopsis eyrei* *Castanopsis fabri*	Ultisols
DH	112°32′14″	23°10′25″	240	21.8	1927	Subtropical monsoon evergreen broad-leaved forest	*Castanopsis chinensis* *Cryptocarya concinna* *Aporosa yunnanensis* *Schima superba*	Ultisols
JF	108°51′26″	18°44′18″	809	23.2	2266	Tropical monsoon forest	*Cryptocarya chinensis* *Mallotus hookerianus* *Cyclobalanopsis patelliformis* *Cryptocarya chinensis* *Gironniera subaequalis*	Ultisols

[a] HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY,Taiyue; SN, Shennong; JL, Jiulian; DH, Dinghu; JF, Jiangfeng.
[b] MAT, mean annual temperature; MAP, mean annual precipitation.

Table 2
Soil properties of different sampling sites.

Sampling site	pH	ST (°C)	SM (%)	Silt (%)	SOC (g kg^{-1})	TN (g kg^{-1})	MBC (mg kg^{-1})	MBN (mg kg^{-1})	Easily soluble P (mg kg^{-1})
HZ	6.79 ± 0.02a	10.3 ± 0.15g	45.3 ± 0.90c	55.87 ± 1.15c	42.29 ± 0.47b	2.90 ± 0.16d	349.69 ± 5.95a	44.42 ± 0.21b	18.62 ± 1.62a
LS	6.17 ± 0.02b	15.9 ± 0.02f	46.9 ± 0.76c	63.98 ± 0.28b	62.08 ± 7.20a	4.59 ± 0.29b	316.46 ± 0.66a	53.43 ± 0.33a	9.53 ± 1.08b
CB	6.37 ± 0.04b	16.0 ± 0.06f	102.8 ± 0.25a	76.18 ± 0.64a	72.38 ± 2.00a	6.05 ± 0.17a	178.42 ± 8.80b	52.33 ± 1.37a	11.91 ± 0.38a
DL	6.87 ± 0.02a	17.8 ± 0.14e	32.4 ± 0.30e	6.35 ± 2.38e	38.83 ± 0.41c	3.17 ± 0.04d	43.25 ± 0.81e	36.26 ± 2.17c	6.59 ± 0.10c
TY	6.85 ± 0.05a	16.0 ± 0.12f	36.0 ± 0.23d	49.39 ± 1.42d	41.34 ± 2.75c	2.43 ± 0.15e	115.46 ± 3.96c	36.67 ± 0.96c	5.25 ± 0.44c
SN	6.93 ± 0.01a	18.4 ± 0.12d	50.5 ± 0.63b	74.08 ± 0.26a	36.13 ± 1.26c	3.76 ± 0.05c	71.60 ± 13.05e	52.01 ± 0.35a	1.33 ± 0.19d
JL	5.57 ± 0.19b	25.3 ± 0.01a	39.0 ± 0.89d	67.74 ± 0.31b	31.55 ± 1.82c	2.28 ± 0.09e	89.08 ± 19.68d	37.41 ± 2.20c	0.21 ± 0.05e
DH	5.43 ± 0.03c	24.4 ± 0.04b	37.8 ± 0.38d	49.74 ± 1.77d	28.47 ± 0.54d	1.77 ± 0.02f	37.96 ± 0.06e	18.89 ± 0.25d	1.21 ± 0.01d
JF	6.32 ± 0.01c	22.5 ± 0.07c	38.6 ± 0.12d	49.21 ± 0.16d	29.38 ± 0.94d	1.99 ± 0.02e	140.39 ± 1.29c	44.17 ± 1.85b	1.85 ± 0.04d

Note: ST = temperature of 0–10 cm soil; SM = soil moisture; Silt = soil silt content; SOC = soil organic carbon; MBC = microbial biomass carbon; TN = soil total nitrogen; MBN = microbial biomass nitrogen; Easily soluble P = soil easily soluble phosphorous. Values were presented as means ± SE (n = 4). Different lowercase letters indicate significant differences between different forests. The abbreviations of the sampling sites are shown in Table 1.

2.3.2. Vegetation data

We recorded all the plant species within each plot, and measured the height and diameter-at-breast-height (DBH) of each woody individual that had a DBH greater than or equal to 2 cm. We calculated the diversity (H′, Shannon-Wiener) of the tree species in the community.

$$H' = \sum_{i=0}^{n} (PilnPi)$$

in which P_i was the important value of the species i, and n was the number of the species.

We determined the TN and TC concentrations of sun-exposed and mature leaves (leaf blades for trees) collected from five to ten individuals of each tree species at each site. We assigned traits to each tree species found in the survey plots. We calculated the SLA (the one-sided area of a fresh leaf divided by its oven-dried mass, $m^2\,kg^{-1}$), LDMC (the oven-dried mass of a leaf divided by its water-saturated fresh mass, $mg\,g^{-1}$), leaf C ($g\,kg^{-1}$) and leaf N ($g\,kg^{-1}$) for ten fully expanded leaves from each individual site. We also calculated the community-weighted means (CWM), as follows:

$$CWM = \sum_{i=0}^{n} Pi \times trait\ i$$

in which Pi was the relative contribution of the species i to the cover of the whole community, n was the number of the most abundant species, and trait i was the trait value of species i, as described by Garnier et al. (2004). The tree species diversity and the plant functional traits are summarized in Table S2.

2.3.3. Phospholipid fatty acid analysis

The PLFA contents of samples were determined using the method described by Bååth and Anderson (2003). Fatty acid methyl esters (FAMEs) were formed by mild alkaline methanolysis, and the samples were dissolved in hexane and analyzed with a DB-5 column in a gas chromatography mass spectroscopy (GCMS) system (Thermo TRACE GC Ultra ISQ). The different PLFA biomarkers were used to represent the different groups of soil microorganisms (Table S2). Taken together, the combination of bacterial, fungal and actinomycic PLFA biomarkers represented the total PLFAs of the soil microbial community.

2.4. Statistical analysis

We used one-way analysis of variance (ANOVA) followed by a post-hoc Tukey HSD test to determine the differences among the soil properties and the sums and ratios of the various microbial lipid groups in the different forest ecosystems. We tested the relationships between environmental variables and different groups of microbial biomass with the Pearson correlation test. The correlations and ANOVA tests were performed using SPSS 19.0 for Windows. All data were reported as means ± SEs. We developed a heatmap in Excel 2013 from the correlation coefficients data and edited it with Adobe Illustrator CS6.

The relationships between the environmental variables and the variations in the structures of the microbial communities were determined by redundancy analysis (RDA) using CANOCO 4.5 (Ter Braak and Smilauer, 2002). The environmental variables included climatic variables (MAT and MAP), soil biochemical variables (ST, SM, C/N, C/P, N/P, SOC, TN and easily soluble P), soil texture (silt content) and plant functional traits (H′, LDMC, SLA, Leaf C and Leaf N). We used Monte Carlo permutations and automatic selection of means to test the significance of the variables. We constructed the biplot from the scaling of RDA1 and RDA2.

3. Results

3.1. Microbial biomass and PLFAs

The average soil MBC concentrations in the boreal forest and the two temperate forests were 349 (HZ), 316 (LS) and 178 (CB) $mg\,kg^{-1}$; these concentrations were between 3 and 9 times higher than the concentrations in the warm temperate and subtropical forests (Table 2). The average soil MBN concentration in the temperate forests was a little higher than 50 $mg\,kg^{-1}$, which was between 1 and 3 times greater than the average in the warm temperate and subtropical forests.

Soil total PLFAs ranged from 7 to 23 $nmol\,g^{-1}$ along the NSTEC, and were highest in CB and lowest in TY and JF ($P < 0.01$). Overall, various groups of PLFAs were higher in the temperate forests than in the warm temperate, subtropical and tropical forests ($P < 0.01$) (Fig. 2(a)). Soil fungal PLFAs ranged from 0.2 to 0.9 $nmol\,g^{-1}$, but did not show an obvious latitudinal gradient. Soil F/B and G^+/G^- ratios in subtropical and tropical forests were higher than those in the temperate and warm temperate forests except DL (Fig. 2(b)).

3.2. Microbial community structures

There were considerable variations in the structures of the soil microbial communities along the NSTEC (Fig. 3). The soil microbial community in the boreal forest was comparable to the communities in the temperate forests (HZ, LS and CB), with high bacteria and actinomycic PLFAs, and were significantly different from those in the warm temperate, subtropical and tropical forests (Fig. 3). The soil microbial communities in JL and DH were similar, but the communities in JL and DH were significantly different from those in HZ, LS and CB (Fig. 3). By examining the PLFA biomarkers of individual microbes, we found that the differences between the microbial structures in the DL forest and the other forests were mainly caused by the high fungal PLFAs (Fig. 3).

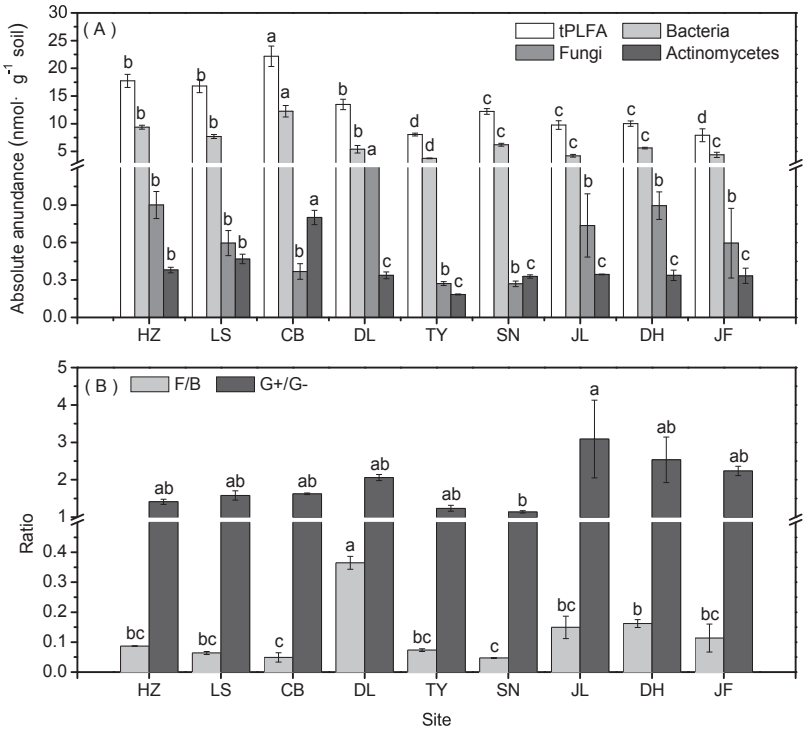

Fig. 2. The contents of PLFAs (A) and ratios of F/B and G^+/G^- (B) in forest ecosystems along the NSTEC. Different lowercase letters indicate significant differences between different forests. F/B, fungi/bacteria; G^+/G^-, Gram-positive bacteria/ Gram-negative bacteria. The abbreviations of the sampling sites are shown in Fig. 1.

3.3. Correlations between soil microbial community structures and environmental properties

Redundancy analyses showed that there were strong positive correlations between the spatial variations in structures of the soil microbial communities and SM, SOC, TN and TP, but strong negative correlations between the spatial variations in the microbial communities and MAP, MAT and ST ($P = 0.002$) (Fig. 3). The RDA2 of the structures of soil microbial community was strongly and positively correlated with the CWM values of LDMC, Leaf N, Leaf C and soil pH, but negatively correlated with the soil silt contents. Overall, MAT and soil nutrients were the main predictors of the variability observed with latitude in the soil microbial communities along the NSTEC, and was consistent with the significant relationships between different groups of PLFAs, soil nutrients and climate (Fig. 4).

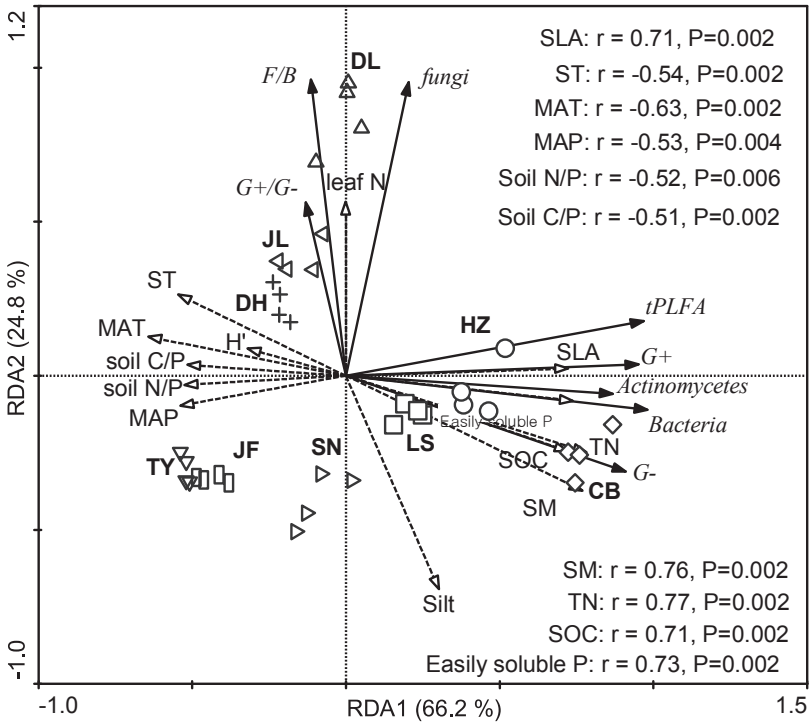

Fig. 3. Redundancy analysis ordination biplot of soil microbial individual phospholipid fatty acids (PLFAs) and environmental properties. The dotted lines and solid lines represent the environmental variables and lipid signatures and carbon sources. The abbreviations of the variables: MAP, mean annual temperature; MAT, mean annual precipitation. The vegetation data were the trait of the tree layer, H′, diversity of tree layer; LDMC, leaf dry matter weight; Leaf C, leaf carbon content; Leaf N, leaf nitrogen content; SLA, specific leaf area. Soil properties included ST, soil temperature; SM, soil moisture; Silt, soil silt content; TN, soil total nitrogen; SOC, soil organic carbon; Easily soluble P, soil easily soluble phosphorous.

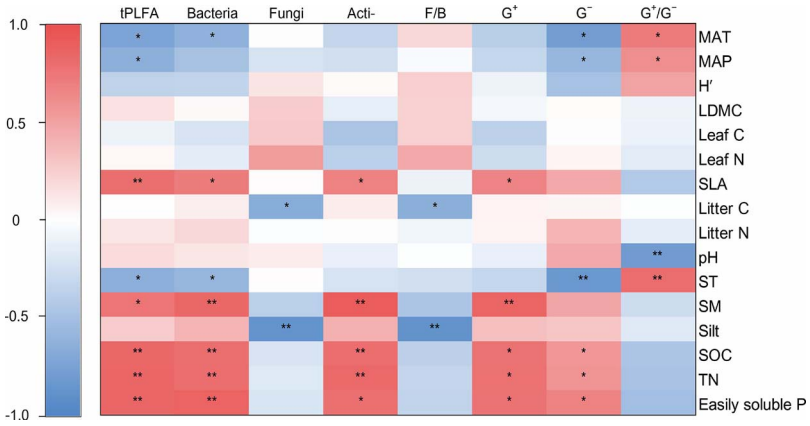

Fig. 4. Heatmap of the Pearson's correlation coefficients between microbial variables and environmental properties. The variables were abbreviated as follows: Acti- = actinomycetes; litter C = litter total content; litter N = litter total nitrogen. The other variable abbreviations are given in Fig. 3. $^{**}P < 0.01$, $^{*}P < 0.05$.

4. Discussion

4.1. Comparisons with previous studies

The soil MBC and MBN values measured are comparable with those reported in previous studies (Hartman and Richardson, 2013; Xu et al., 2013). The average MBC values estimated by Xu et al. (2013) at depths of up to 30 cm in the soil profile in their summary of different forest soils at the global scale, with 95% confidence boundaries of between 360 and 1512 mg C kg^{-1}, were consistent with those reported for the temperate forests (HZ, LS) but were higher than those reported in the other forests (Table 2). The average MBN concentrations in this study ranged from 18 to 60 mg N kg^{-1} and were comparable with the global estimates reported by Hartman and Richardson (2013). The total PLFAs in subtropical forests estimated by Liu et al. (2012) were much higher than those derived in this study, and were different from our values because we used different PLFA biomarkers to represent total PLFAs.

The values of the soil MB to soil total elements ratio that we calculated differed from those reported by other researchers (Xu et al., 2013). In this study, fractions of SOC and soil TN ranged from 0.2 to 1.0% and 1.0 to 3.0%, respectively, but ranged from 0.9 to 6.5% and from 1.7% to 8.1%, respectively, at the global biome level (Xu et al., 2013). The differences between our values for the forests along the NSTEC and those of Xu et al. (2013) reflect the fact that their average values were calculated from a larger and more complete dataset that covered all the major biomes worldwide.

4.2. Latitudinal gradient of microbial biomass and structures

Our results showed that there was a general latitudinal gradient in MB, soil bacterial PLFAs and soil nutrient concentrations, which indicates that bacteria prefer fertile soils (Ingwersen et al., 2008), while fungi prefer acidic soils with low nutrient availability (Taylor et al., 2010). Therefore, the soil fungal PLFAs and F/B ratios were highest in subtropical and tropical forests where the soil nutrient levels and soil pH were lowest (De Vries et al., 2012). Soil G^+/G^- ratios were highest in the subtropical forest where G^- bacteria PLFAs were least abundant, which may reflect microbial growth strategies. The G^+ bacteria are primarily K-strategists that can survive over long periods in the soil under harsh conditions (Andrews and Hall, 1986). In contrast, soil G^- bacteria are known to be primarily r-strategists, and are important for the decomposition of fresh litter material (van Gestel et al., 1993). Our results confirm that the soil nutrients were low and litter inputs decomposed rapidly in the subtropical forest soils, so the conditions were not beneficial for G^- bacteria.

Soil microbial communities differed among the forest types and varied considerably along the climatic gradient. Consistent with previous studies, soil microbial communities in forests in the same climatic zones were similar (Wu et al., 2009; Brockett et al., 2012). For example, Brockett et al. (2012) reported that the structures of soil microbial communities varied among seven forests along a climatic gradient in Canada. Wu et al. (2009) reported biogeographical trends, and demonstrated with cluster analysis that the structures of soil microbial communities were separated into three groups. Fierer et al. (2009b) found that variations in MB obtained using the chloroform fumigation-extraction (CFE) technique could be predicted across biomes at the global scale. Using molecular techniques, Tedersoo et al. (2012) and Fierer et al. (2009a) found that there were obvious spatial patterns across climate zones and soils, respectively.

4.3. Mechanisms driving latitudinal variations in microbial biomass and structures

In our study, soil nutrient concentrations and climatic factors were good predictors of the latitudinal variations in the compositions of soil microbial communities. Soil nutrients are fundamental for microbial growth and different microbial functional groups favor substrates of varying quality, which means that, as reported by Wallenius et al. (2011) and Frossard et al. (2013), the structures of soil microbial communities may be influenced by the soil C concentrations, and that soil bacterial biomass may be higher in forests with high soil organic matter concentrations (Wallenius et al., 2011). The fact that soil tPLFAs were positively correlated with soil MBC, MBN, SOC and TN concentrations is consistent with the earlier findings (Fig. 5). When C in plants is limited, SOC, but not C in litter, can also be an important source of C for soil microbes (Frossard et al., 2013). Concentrations of SOC were between 72.4 and 28.5 g C kg^{-1} soil and TN concentrations were between 6.1 and 1.7 g N kg^{-1} soil, in the temperate and tropical forest soils, respectively, and were lower in the tropical forests than in the temperate forests (Table 2). Apart fungal PLFAs, the trends in the PLFA biomarkers were similar. Phosphorus, a limiting element in many regions (Xu et al., 2017), can stimulate different groups of soil PLFA microbes and MB (DeForest et al., 2012; Dong et al., 2015). Therefore, phosphorus also contributed to the variations in soil microbial communities in our study.

Climatic factors (MAT and MAP) were generally strongly correlated with the variations in microbial communities, which is consistent with the findings of Tedersoo et al. (2012) and Zhou et al. (2016), who found that MAT and MAP explained most of the variations in the compositions of soil microbial communities. Forests in same climatic zones are reported to be similar in terms of microbial communities (Fierer et al., 2009a). The NSTEC represents a latitudinal and temperature gradient along which the MAT varies from –3.7 to 23.2 °C and the MAP ranges from 473 to 2266 mm. Spatial heterogeneity in climate conditions leads to large variations in soil biogeochemical properties, with consequences for the distributions of microbes (Kumar et al., 1992); other variables that vary with latitude, such as ST and SM, may also influence soil microbial communities (Carletti et al., 2009). When the soil

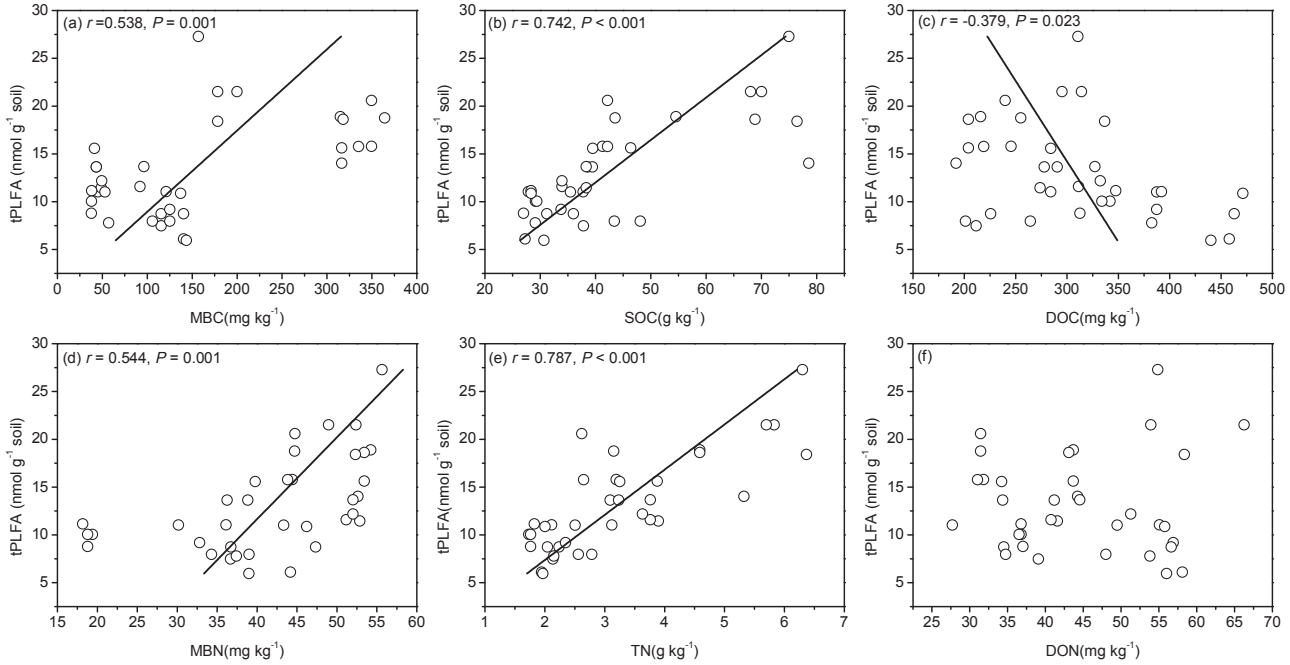

Fig. 5. Relationships between total PLFAs and different forms of soil C and N.

temperature is higher than the optimal level, soil microbes will be eliminated from the environment. The strong relationships between SM and ST and the ordination axes in this study indicate that soil microbial communities also varied as SM varied (Brockett et al., 2012). For example, Kieft et al. (1987) reported that soil microbial cells could dissolve as SM increased, but that cell plasmolysis could occur when SM decreased (Rosacker & Kieft, 1990).

To date, several studies have reported that below-ground microbial communities are associated with different plant functional traits (Kivlin and Hawkes, 2016; Pei et al., 2016; Tu et al., 2016; Zuo et al., 2016). In contrast, we found that the latitudinal pattern of soil microbial communities was independent of most plant functional traits apart from SLA. Soil microbial communities may be dominated by bacteria when the plant species have high SLA, high leaf N concentrations and low LDMC values (Orwin et al., 2010). The close linkages between the patterns in plant and microbial communities appear to follow the leaf economic strategy (De Vries et al., 2012; Wright et al., 2004). Slow-growing plants in N-poor environments, with low SLA and leaf N concentration, are associated with fungi-dominated microbial communities that can decompose low quality plant litter (Wright et al., 2004). There were no causal links between SLA and fungal PLFAs in our data, but the positive relationships between the SLA and both soil tPLFAs and bacterial PLFAs are consistent with the earlier findings (Fig. 4). If we look beyond individual traits, related tree species could possibly cultivate similar microbial communities through co-evolution of plants and microbes (Liu et al., 2012).

Various other factors, such as soil pH and soil silt content, had only minor influences on the geographical patterns of soil microbial communities. The bacterial diversity increases as pH increases, which causes the soil microbial community to transition to one with more G^- and fewer G^+ bacteria PLFAs (Wu et al., 2009; Shen et al., 2013). While we observed similar trends in our study, we also found that soil pH did not determine the microbial community, perhaps because the PLFA analysis of the microbial community did not represent all the microbial groups in the soil (Xu et al., 2013). Soil bacterial PLFAs were higher in temperate forests where the soils were fine-textured and had silt contents between 50% and 80%. Fine-textured soils are generally more favorable for bacterial growth because they have greater water-holding capacity and nutrient availability, and are better protected from bacterial grazers (Carson et al., 2010).

5. Conclusions

In conclusion, we found that soil MB and microbial communities showed biogeographic variation and were generally organized along a gradient over a large geographical area, and that forests in the same climatic zones had similar microbial properties. The latitudinal variations in the soil microbial communities were closely related to soil TN, SOC, easily soluble P and MAT, and were weakly associated with SM, ST and the CWMs of SLA. Our results suggest that soil properties, but not plant functional traits, drive the development of soil microbial communities. To the best of our knowledge, this study is one of the first to report variations in the environmental controls on the structures of soil microbial communities along a latitudinal gradient in China's forest ecosystems, and this information will support the development of a generalized model framework that will provide improved simulations of microbial mechanisms in C cycling. By including the generalized algorithm that controls MB and community structure in ecosystem models, we could then make more accurate predictions of the microbial mechanisms that influence C and nutrient cycling (Xu et al., 2014).

Data accessibility

Requests for data and materials should be addressed to N.H. (henp@igsnrr.ac.cn) and G.Y. (yugr@igsnrr.ac.cn).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the

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